54. On the Colours of Water-Mites. By C. S. Elton, New College, Oxford *.

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1. Introduction.

There are in the British Isles over 250 species of Hydrachnidæ or Water-mites, belonging to about 40 genera [7]. The life-history is interesting, as the larva is usually parasitic upon some other fresh-water animal (e. g., *Hydrachna globosa* or *Dytiscus*, *Nepa*, etc.), although the adult is free-living. By such means dispersal is often effected. One result of this rather elaborate and risky life-history is that comparatively few adults are usually found. We should expect, *a priori*, to find some special method of defence among these mites, since they are not able to increase rapidly in numbers, in order to counteract the depredations of enemies.

The colours of Water-mites are very varied. As this paper deals mainly with the scarlet species, the genera may be roughly divided into four groups in order to give some idea of the colours which occur :

1. All the species of the genus bright red, e. g., *Eylais*, *Diplodontus*, *Hydryphantes*, etc.
2. Most of the species of the genus bright red, but a few non-red, e. g., *Hydrarachna*.
3. A few of the species of the genus bright red, but most of them non-red, e. g., *Limnesia*, *Arrhenurus*, *Piona*.
4. All the species of the genus non-red, e. g., *Atax*, *Hygrobates*. This is a large group and the colours are extremely varied.

(These groups are not intended to express the natural relations of the genera.)

The ground-colour of the mites is due to pigment present in the skin. Markings of various sorts are produced by the internal organs showing through the skin.

It is the object of this paper to prove that warning coloration and probably Müllerian mimicry exist among some at least of the Hydrachnidæ.

I am much indebted to Prof. E. B. Poulton for help and encouragement during the preparation of this paper, and to Mr. C. D. Soar for help in identifying the mites, and for other valuable information mentioned later on.

* Communicated by Professor E. B. Poulton, F.R.S., F.Z.S

2. The Mites of Railway Ditch, Oxford.

If there are no particular laws governing the occurrence of colours in mites we should expect to find chance mixtures of colours among the species of any one habitat. In the following example such was clearly not the case. During May 1921 the fauna of a small ditch near Oxford (here referred to as "Railway Ditch") was examined by me. This ditch is connected by several channels with the Thames, but is usually almost stagnant. Only one part of it was studied, an area about 30 yards long and 4 feet wide Since it is important to know what animals and plants are associated with the mites, a list of the species observed during the course of the work is given below. This list is not by any means exhaustive, but gives some idea of the type of habitat in which the mites were living.

Plants: *Ranunculus aquatilis* Agg., *Hottonia palustris* L., *Callitriche aquatica* Sm., *Potamogeton natans* L., *P. perfoliatus* L., *P. densus* L. (*Lemna minor* L., *L. trisulca* L.).

Hirudinea: Two large species.

Mollusca: *Limnæa stagnalis* L., *L. peregra* Müll., *Planorbis corneus* L., *P. complanatus* L., *P. spirorbis* Müll., *Ancylus lacustris* L., *Bithynia tentaculata* L., *Paludina vivipara* L.

Insecta:

Coleoptera: *Dytiscus marginalis* L., *Hyphrydus ovatus* L., *Hydroporus palustris* L., *Agabus bipustulatus* L., *Haliplus* sp.

Hemiptera: *Nepa cinerea* L., *Hydrometra stagnorum* L., *Notonecta glauca* L., *Corixa* sp., *Velia* sp., *Gerris* sp.

Neuroptera: Various larvæ.

Crustacea: *Cyclops serratulus* Fischer, *C. prasinus* F.
Chydorus sp.
Asellus aquaticus L.

Fish: *Gasterosteus aculeatus* L.

Amphibia: Frog tadpoles.

The mites and their colours are shown in Table I.

Table I.—The Mites of Railway Ditch, May 1921.

Species.	Colour.
Hydrarachna globosa De Geer.	Scarlet.
H. schneideri Koen.	Scarlet.
H. distincta Koen.	Scarlet.
H. fuscata Soar.	Dark purple with reddish spot on back.
Eylais hamata Koen.	Scarlet.
Diplodontus despiciens Müll.	Scarlet.
Hydryphantes ruber De Geer.	Scarlet.
Piona longipalpis Krend.	Scarlet with black spots on back.
Limnesia fulgida Koch.	Scarlet with black marks on back.

The ditch was full of breeding 3-spined Sticklebacks (*Gasterosteus aculeatus*). The males were guarding their nests and driving off all intruders fiercely. The mites were not abundant, only about 20 specimens being taken, after a good many days of watching and collecting. This fact made it impossible to do as many experiments as one could have wished. When a scarlet mite did appear, it was extremely conspicuous and sometimes swam near a male fish without being touched.

3. The Evidence for Warning Coloration.

Experiments were made in May 1921 in order to see whether mites are eaten by Sticklebacks.

Expt. 1. A large male 3-spined Stickleback from Railway Ditch was placed in a vessel of water, and starved for three days. It was then offered a *Daphnia pulex*, which it devoured. Directly afterwards a *Limnesia fulgida* was put in. The fish made towards it from an inch or two away, but stopped half or quarter of an inch from it and swerved off. It repeated this after a minute or two. After that the mite was disregarded altogether. When given another and brighter *L. fulgida* the fish went up to it once in the same way, and afterwards ignored it. It was given another *Daphnia* which it devoured eagerly.

Expt. 2. The last experiment was repeated on the same fish, *Eylais hamata* being used instead of *Limnesia*. The mite was completely ignored after several inspections.

Expts. 3, 4, 5. The same result was obtained when *Diplodontus despiciens*, *Piona longipalpis*, *Hydrarachna distincta*, respectively, were used.

These experiments show that the fish avoided scarlet mites even when it was fairly hungry, that the latter were presumably distasteful to it, and that the fish remembered this fact from its former experience.

Expt. 6. A Stickleback was placed in a vessel as before. A *Daphnia* was eaten eagerly. An *Eylais hamata* was put in and avoided by the fish. Another *Daphnia* was eaten. A *Hydrarachna fuscata* was now introduced. The *E. hamata* accidentally bumped into the fish, which whipped round and snapped up the mite, but immediately spat it out again. The fish then approached *H. fuscata* but did not touch it. A *Daphnia* was then put in and eaten.

This experiment shows that *E. hamata* was actually distasteful to the Stickleback, and that *H. fuscata* was avoided.

Mr. Soar tells me that he has never seen any mite eaten except by other mites. He once observed a *Dytiscus* larva which refused to touch a *Diplodontus despiciens*. Piersig [3] quotes an observation of Dugès to the effect that *Nepa* refused to touch water-mites, but does not state what species. Thus, scarlet mites are avoided by two of the fiercest enemies of fresh-water animals, *Dytiscus* and Sticklebacks, both of which were present in

Railway Ditch. [Mites will often attack each other. *Piona longipalpis* was seen to attack *Limnesia fulgida* and *Hydrarachna fuscata*, and Mr. Soar states that *L. fulgida* will often attack *Eylais*.]

Hydrarachna fuscata, which is not scarlet, has the peculiar habit of crumpling up its legs and feigning dead when touched. Mr. Soar states that he does not know of any other Water-mite which does this, although mites sometimes are found resting in a crumpled up position. Before we can say what the precise use of this habit is, more experiments are required. But the following occurrence shows that it may be an advantage sometimes.

Expt. 7. A *Hydrarachna schneideri* and a *H. fuscata* from Railway Ditch were put in a jar with a specimen of *Agabus bipustulatus* from a pond in Oxford Botanic Gardens in which no mites had ever been seen, although regular collections had been made for nine months. The beetle attacked and ate *H. schneideri*. Meanwhile *H. fuscata* feigned dead during the disturbance and remained unharmed.

This experiment does not prove anything with regard to the distasteful properties of *H. schneideri*, since the beetle was almost certainly unused to scarlet mites.

Expt. 8. In the autumn of 1921, a young 3-spined Stickleback from a flood-pond near Railway Ditch was starved for three days and then given a *Tubifex*, which it gobbled up. A *Limnesia fulgida* from Railway Ditch was put in with it. The fish dashed at the mite and caught hold of one leg, but immediately let go and left it. After this the fish went up to within a quarter of an inch of the mite several times, but did not touch it. The mite was left in with the fish for seven days, but still remained uneaten, although the latter had now been starved for ten days.

Expt. 9. In the end of February 1922 a young 3-spined Stickleback was taken in Railway Ditch and was starved for four days. (No mites were to be found in the ditch at this time.) A *Simocephalus vetulus* was put in and eaten eagerly. A nymph of *Hydrarachna paludosa* Thon. from a salt stream at Marcham was now put in. This species is coloured very brilliant scarlet. The fish went up to it and took the mite into its mouth, but immediately spat it out. It went up to the mite repeatedly after this without eating it, and followed it round for some time, clearly torn between its ravenous hunger and the unpleasantness of the mite. The latter was now removed.

Two days later, the Stickleback (having now been starved for six days) was given two *Simocephalus*, which it devoured. *H. paludosa* was then introduced. This time the fish snapped up and spat out the mite many times, but sometimes avoided it, and never swallowed it.

This experiment shows among other things the effect of hunger on the reactions of the fish.

All Water-mites possess large skin-glands, provided with so-called "sensory" hairs, whose function has been, so far, uncertain. As Piersig (3) points out, it has long ago been suggested that these glands secrete some unpleasant fluid; but he states that there is not enough evidence to decide whether the mites are distasteful or not. That they are so to Sticklebacks is certain, in view of the experiments here described. The idea that it is the skin-glands which make the unpleasant taste, is supported by the fact that the fish does not injure a mite when it takes it into its mouth, and therefore cannot actually taste its flesh; also by the fact that the mite is spat out so promptly. The anatomy of these glands and the nature of the supposed secretion require to be worked out in detail. The hardness of the body probably helps to render some mites distasteful, as indicated by the fact that a Stickleback when not very hungry will sometimes reject a young *Asellus*, after taking it into its mouth. But this could not apply to such soft-skinned mites as *Eylais* and *Diplodontus*.

These experiments make it clear that Sticklebacks recognize the scarlet mites by their appearance. It is extremely likely that it is the colour which is remembered, although no accurate work has been done on *Gasterosteus*, in order to prove this. But White (8) has recently shown that the American Stickleback (*Eucalia inconstans*) and Mud Minnow (*Umbra limbi*) are well able to distinguish differences in colour as distinct from differences in the intensity of light. She proved by experiment that the fish were capable of associating different colours with their food, though they were unable to distinguish between fine shades of the same colour. The same may well be the case for the 3-spined Stickleback.

There is another point which is of some importance. It may be asked what advantage is gained by mites, seeing that they appear to be uninjured by fish, even after being snapped up and spat out several times. The answer to this is that: (1) Mites must be actually destroyed by some animals before their distastefulness can be realized, e. g. *Agabus*; (2) the fluid which seems to be secreted by the skin-glands would ultimately become exhausted; (3) being continually attacked must interfere with the life processes of the mite. The degree of effectiveness of warning colours depends among other things on the state of hunger of the enemies.

4. The Evidence for Müllerian Mimicry.

There is no evidence at present of Batesian mimicry, *i. e.* of edible mimics, among Water-mites. It is unlikely that it exists, in view of the facts that all Water-mites have the large skin-glands and that there are very few cases on record of mites being edible. However, the possibility should not be ignored. There is, on the other hand, strong evidence of Müllerian mimicry among mites. It seems remarkable that eight species of scarlet mites belonging to six genera occurred in Railway Ditch. Two of these species are members of genera in which the other species are mostly non-red (*Limnesia* and *Piona*). The only species which is not bright red, occurring in the ditch, has a special defensive habit, not found among other mites. The absence of any other non-red species is remarkable, since there is no dispersal difficulty to prevent them from immigrating from the Thames. The shape, size, and mode of swimming of all these species are much the same, except that *Eylais* trails its legs behind.

If we exclude the possibility of coincidence, the explanation might be that the red mites possess some advantage which is not shared by the non-red ones. Now, there may be two important factors affecting the evolution of a group of animals in the direction of having a common colour :—

(1) In the words of Prof. Poulton, "the feasibility of certain colours and patterns depending upon their effect on the vertebrate eye and thus giving the enemies as easy an education as possible" (4). That is to say, scarlet may have a more striking effect on the retina of the Stickleback's eye than any other colour, and therefore be more effective as a warning.

(2) Reinforcing this would be the co-operative advantage of Müllerian mimicry as usually understood.

The early stages in the evolution of a set of Müllerian mimics would be easier to conceive of if there was any evidence that the first factor is an important one, and its effect would be greater in the case of animals which, like these scarlet mites, are of one uniform colour and do not possess elaborate patterns. (The latter, where they occur, cannot be explained without the aid of the Müllerian theory.) Therefore, if it can be shown that Sticklebacks remember scarlet mites better than those with other colours, the case in favour of Müllerian mimicry will be correspondingly strengthened. The following experiments show that this may be so :—

Expt. 10. The same fish was used as in Expt. 9, after being starved for four days. As was seen in that experiment, a scarlet *Hydrarachna paludosa* was refused after one trial. A *Simocephalus* was then put in and eaten at once. A specimen of *Hygrobates longipalpis* Herm. was introduced. This mite is coloured black and yellow, and is quite conspicuous. The fish snapped it up and immediately spat it out. This it repeated fourteen times at intervals. Another *Simocephalus* was put in and eaten. The mite was again taken in and rejected seven times. Another *Simocephalus* was eaten. The fish now approached the mite four times without touching it. After that the mite was more or less ignored. A *Limnesia undulata* Müll. was now put in. This species is yellow with black or brown spots. The fish took it in its mouth and spat it out twice, and afterwards avoided it. *Hydrarachna paludosa* (brilliant scarlet) was now introduced, and the fish avoided it after one trial. There were also some *Cypris virens* present, coloured a uniform brownish green. This Ostracod was too hard for the fish to crush and too big to swallow; yet the Stickleback kept rushing at the *Cypris* whenever they moved, trying to swallow them. This it continued to do throughout several days.

This experiment suggests that scarlet was remembered by the Stickleback better than yellow and black, although the hunger of the fish has to be taken into account. But both were more effective than the dull uniform colour of the *Cypris*.

Expt. 11. The same fish was used as in Expt. 1. It was experienced as regards scarlet mites. A *Daphnia* was eaten eagerly. An *Acercus lutescens* Herm. was put in. This is a small mite, coloured pale pink, dark brown, and yellowish white. The fish snapped up the mite, but immediately spat it out again. This was repeated three times. After this the mite was avoided. A short time afterwards the fish noticed it again, and the whole procedure was repeated (the same number of times). A *Daphnia* was eaten. *Eylais hamata* (scarlet) was introduced, but avoided after inspection. Both mites were removed. Next morning the experiment was repeated. The fish saw *Acercus* and snapped it up, and then spat it out. Next time the mite was avoided. The mite was then removed. Thirty-five minutes later *Acercus* was put in again. The fish went right up to the mite, but did not touch it. After this the mite was ignored. *Daphnia* was put in and eaten. *Eylais* was put in and avoided. This experiment suggests that the fish was able to remember the scarlet much better than the other colours. It is unlikely that the difference in impressions made on the fish was due to the scarlet mite having a more unpleasant taste than the other, since both were spat out equally promptly. It is probable, then. that scarlet is the most efficient warning colour for use in Stickleback-haunted habitats. Perhaps it is only the best for such habitats at one time of year, *i. e.* in the breeding-season of the fish. I observed yellow-and-black mites (unidentified) in a Hampshire pond where 3-spined Sticklebacks occurred on August 4th, 1922. This shows that such mites can exist in some Stickleback ponds. Not much is known about the food reactions of these fish, except that they are usually very fierce and voracious. It is necessary to be very cautious in applying the knowledge about food habits of Sticklebacks in one place to those of another. J. T. Saunders (5) records a pond in which the adult 3-spined Sticklebacks ate nothing but one kind of diatom, while the young ones in the same pond and all the fish of neighbouring ponds were carnivorous. He also states that the fish soon learn to distinguish by sight between different animal foods, and that they are very sensitive to changes in their environment—*e. g.*, the diatom-eaters became carnivorous in captivity. The latter fact might throw some doubt on the validity of the experiments with mites etc. described here; but the uniformity of the results makes it pretty certain that the fish would reject Water-mites in nature as well as in captivity.

The fact that the fish in Expts. 10 and 11 did not learn well on other colours than scarlet does not weaken the case in favour of warning coloration, since the non-red mites used were not in the presence of their natural enemies. *Acercus lutescens* came from a pond in which there were no fish. *Hygrobates longipalpis* and *Limnesia undulata* were from the Thames. Now, although Sticklebacks are abundant in most rivers, Maxwell (2) says: "It has been observed that the Stickleback is very scarce in the Thames."

The chief importance of these non-red mites here is that it has been shown that they might be at a disadvantage in Stickleback-haunted habitats (where scarlet ones are successful), and that non-red mites actually tend not to come in such places.

Some other evidence may be added to this, though very little is known about the associations of Water-mites.

There is a flood-pond near Railway Ditch which was full of 3-spined Sticklebacks in May 1921 (see Expt. 8). The very large and conspicuous scarlet *Eylais extendens* Müll. was taken here swimming about among the fish. The only other mite was *Piona conglobata* Koch, which is very minute and is inconspicuously coloured. *Hyphrydrus ovatus* was unusually abundant in Railway Ditch in May 1921. This beetle is coloured bright orange below. It secretes a liquid when handled, which smells like honey and may make it distasteful. It is possible that the Müllerian mimicry included this beetle. Shelford (6) records *Limnochares aquatica*, which is a large scarlet mite and is unable to swim, as occurring abundantly in a pioneer association of Chara, in which were also many species of fish. Mr. Soar tells me that all the crawling Water-mites are red, which supports the idea that they are warningly coloured.

5. Discussion.

Scarlet is rather rare among animals, except in the tropics. Higgins (1) has suggested that it is due to the fact that red rays are more valuable (there being more energy per unit wave-length than in other colours of light), and are therefore usually absorbed, not reflected. It is more likely that the rareness of scarlet is due to its conspicuousness when seen against natural browns and greens (as in our own road-traffic warning signs). In any case, we generally find that animals are scarlet only when there is some very important use for the colour. For the reason given above, it makes an excellent warning colour. It is possible that red can be seen from further away in water than other colours. This is known to be the case in air.

Any protection gained from warning coloration and Müllerian mimicry would be, of course, only relative. For instance Piersig quotes Forbes, who found that fish did not entirely refuse to eat Water-mites, and gives as his own observation that *Ranatra* seized and sucked mites without hesitation (3), but does not state whether these were the natural enemies of the mites. Before any generalization can be made about the colours of Water-mites, more information is required about their associations, together with experiments in which their natural enemies are used. Mr. Soar states that many mites vary in colour individually a great deal (e. g. *Piona rufa* Koch). It is quite likely that the colours of other mites than those described here may have some different significance.

In conclusion it may be pointed out that many Land-mites are bright scarlet, and no experiments appear to have been done on them.

6. Summary.

1. Ecological observations are described which make probable the existence of warning coloration and Müllerian mimicry among certain species of Hydrachnidæ.

2. Experiments are described which show that these are distasteful to and recognized by Sticklebacks (*Gasterosteus aculeatus*).

3. There is evidence that scarlet is the colour best remembered by these fish. This makes the evolution of such a set of Müllerian mimics more easy to understand.

4. Other evidence is given in support of these conclusions.

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